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Different motor systems use similar damped extraretinal eye position information

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Abstract

Extraretinal eye position information (EEPI) shifts the directional significance of retinal loci by an angle roughly equal to that of an associated saccade, with the shift reported to begin 0–250 ms before the saccade and to continue apace with the saccade, or sluggishly, over a period as much as an order of magnitude longer. These different estimates of remapping initiation and duration could be due to various factors, including different localizing responses, retinal loci of probe flashes, and saccade target predictability. We compared manual and gaze pointing to probe flashes at controlled retinal loci under identical stimulus conditions and in the same subjects, and found that EEPI was similar: both hand and gaze pointing EEPI shifted over about 140 ms, beginning about 50 ms before the saccade. For both pointing responses, remapping appeared to be initiated later for parafoveal loci than for loci 10° to either side. We found no effect of saccade target predictability. We show that variability in EEPI and sensory processing only slightly ($\sim 5\%$) inflates estimates of EEPI shift duration. Based on our results, and comparisons with recent studies, we argue that similar EEPI parameters apply to hand pointing, eye pointing and visual comparisons, and that remaining differences across studies can reasonably be attributed to differences in stimulus conditions.

Keywords: Localization; Saccade; Visual direction; Visuomotor coordination

1. Introduction

Egocentric localization of visual targets presented briefly around the time of saccadic eye movements depends on sensory information about target location on the retina combined with information about gaze direction. Judgments involving only retinal position information, such as common vernier acuity, are much more accurate (Westheimer, 1982), implying that the large errors in egocentric localization result from the calculation involving extraretinal eye position information (EEPI).

Most studies find that saccade-related remapping of retinal position begins sometime during saccadic latency (the period after the saccade initiation cue and before the saccade onset), and stabilizes over a period up to 20 times that of the saccade. Matin and colleagues (Matin & Pearce, 1965; Matin, Matin & Pearce, 1969; Matin, Matin & Pola, 1970; Matin, 1976) had subjects localize a brief probe flash relative to the initial fixation point or saccade goal, and found that EEPI begins to change 100–200 ms before the saccade, reaching a stable value several hundred ms after the saccade. In contrast to such 'damped' or 'sluggish' EEPI, Hallett and Lightstone (1976a; 1976b) found very accurate saccadic gaze pointing (saccades back to perisaccadic targets), and Hansen and Skavenski (1985) found very accurate manual pointing to the locations of probes flashed during a saccade. The results of many other studies (Matin & Pearce, 1965; Matin et al., 1969; Matin et al., 1970; Monahan, 1972; Matin, 1976; Mateeff, 1978; O' Regan, 1984; Honda, 1991; Dassonville, Schlag & Schlag-Rey, 1992; Honda, 1993; Dassonville, Schlag & Schlag-Rey, 1995) fall between these extremes.

Next we discuss several possible factors that contribute to different EEPI estimates.

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1.1. Manual pointing and gaze pointing

Most recent studies have measured visual direction using manual or gaze pointing, rather than visual comparison, perhaps because motor responses minimize complicating visual interactions (Matin & Pearce, 1965; Miller & Bockisch, 1997). It is possible to imagine that, apart from effector-specific artifacts (e.g. mechanical constraints), all such pointing measures reflect the same EEPI. However, there are many other ways EEPI might be provided to different pointing systems, e.g. a common signal might be differently filtered or mixed with other signals, independent signals might carry different EEPI, or independent signals might be calibrated to carry similar EEPI.

It is not clear whether motor systems use shared or independent sources of EEPI. Early studies of manual pointing (Hansen & Skavenski, 1985) and gaze pointing (Hallett & Lightstone, 1976a,b) found similar and accurate EEPI, but have not been replicated. Dassonville et al. (1992) had subjects make saccades to visible targets and look back to the location of a brief flash, and found that EEPI starts to change up to 250 ms prior to the saccade, reaching a stable value in 124–368 ms. In a similar paradigm, Honda (1991) found EEPI began to change about 100 ms before a saccade, continuing for about 200 ms. Miller (1996) had subjects manually point to perisaccadic probes, and reported inaccuracies similar to those of the gaze pointing studies, except that EEPI change appeared delayed. However, we have since discovered that one aspect of this report is in need of correction, and we provide that re-analysis here.

1.2. Visual referents

Visible referents certainly affect perceived direction, perhaps by providing retinal information about the timing and size of saccades, as well as by providing object-relative cues for location. Matin and Pearce (1965) found that the location of visual stimuli flashed within 200 ms of each other are judged solely on the basis of relative retinal location. Sperling and Speelman (reported in Sperling, 1990) conclude that perisaccadic flash localization in the presence of visual referents is determined primarily by visual factors. Dassonville et al. (1995) found that exocentric cues reduced pointing errors, and Honda (1993) found that the duration of remapping with a dim background was less than half the duration with no background. Ross et al. (Morrone, Ross & Burr, 1997; Ross, Morrone & Burr, 1997) found translation and compression of perceived space prior to saccades when saccade targets and frames of reference were visible, whereas the many similar experiments without visible reference frames show translation, but no compression of space. Recent experiments show that extraretinal sources of information are not suppressed by retinal sources when they conflict (Cai, Pouget, Schlag-Rey & Schlag, 1997; Rine & Skavenski, 1997). It seems that the weight given to different sources of information depends on task and stimulus factors.

1.3. Retinal inhomogeneities

Even with visual referents eliminated, there is a sensory issue concerning characteristics of the to-be-localized probe stimulus. Inhomogeneities across the retina make it important to control the retinal locus of probe flashes. If retinal or cortical sensory processing varies with retinal locus, then EEPI measurements could vary with probe location. It might be expected, for instance, that a delayed visual signal would interact centrally with a later phase of the saccadic EEPI signal. This would make EEPI shifts begin earlier with respect to probe flash presentation time. Bischof and Kramer (1968), O' Regan (1984) and Miller (1996) reported that EEPI varied with the retinal locus of stimulation.

1.4. Saccade target predictability

If the saccade causing the shift in EEPI is predictable in direction and magnitude, it might be possible to initiate EEPI shifts earlier than if saccades are random. Various oculomotor centers, such as area LIP (Mazzoni, Bracewell, Barash & Andersen, 1996) and the frontal eye fields (Bruce & Goldberg, 1985), become active between target presentation and movement cues. Prior knowledge of target location may accelerate saccade programming. There have been no studies of whether EEPI is similarly affected by target predictability.

1.5. Statistical damping

Most methods of measuring EEPI sample one point on each trial and combine the data of many trials into an estimate of the complete EEPI time course. Variation in the phase of EEPI relative to the saccade, or in the phase of retinal events relative to a visual stimulus, would cause average EEPI to have a longer time course than the actual signal associated with any single saccade. EEPI variability has been proposed to explain the large increase in detection of displacements during saccades (Li & Matin, 1990a,b). Miller (1980) showed that retinal information reduced variability of total eye position information about saccade size by roughly 40%.

Variability, however, seems unlikely to account for all of EEPI's sluggishness. It is easily observed, and has been quantified by Grüsser, Krizic and Weiss (1987), that the perceived movement of an afterimage lags behind and moves slower than its saccade. Thus, EEPI for a single saccade is damped. Here we estimate the

combined effects of EEPI and visual processing variability on measured EEPI mean duration.

1.6. This study

The overall aim of the present study was to clarify the timecourse of saccadic EEPI. Our experiments measure two kinds of motor EEPI, associated with hand pointing and gaze pointing, providing direct comparisons within the same paradigm and with the same subjects. We minimized exocentric cues, controlled retinal loci of probe flashes, and varied saccade target predictability.

The manual pointing study of Miller (1996) reported that EEPI began to show saccade-related change an average of 2 ms after the saccade began, if an exponential function was fit to the pointing data, and an average of 15 ms before the saccade if a three-piece-linear function was fit. However, we have since discovered that the eye position monitor used in that study reports eye position with an 11 ms delay, which, with the 1 ms delay in the control computer, gave a 12 ms period prior to the beginning of saccade detection during which probe flashes were presented under the mistaken assumption that the eye had not yet begun to move. This short period of delay-induced 'back pointing' distorted the curve fits and saccade-related change initiation times. Those data are re-analyzed herein.

2. Experiment 1: saccades to eccentric locations

To avoid the complexity of retinal-extraretinal interactions, we had subjects make voluntary saccades in complete darkness, and then point to the apparent locations of brief perisaccadic flashes. Auditory stimuli cued fixation and saccades, and visual probes were brief and small.

2.1. Apparatus

Miller (1996) described the equipment in detail. Briefly, we monitored horizontal position of the right eye with a diffuse IR limbus-reflection device (ASL EyeTrac-210). Our subjects viewed monocularly, with left eye patched and head stabilized on a dental impression. We used an infrared camera and video monitor to align the eye position monitor. Before and after each block of trials subjects fixated 9 horizontal LEDs, covering the eye position range of interest. The initial calibration was used during data acquisition, and the average of initial and final calibrations for off-line analysis. We achieved accuracy of at least 1/4° for static eye position.

To estimate signal delays in the ASL EyeTrac-210, we powered two LEDs with a signal generator set to produce saccadic waveforms, pointing one LED at the eye tracker's photodiode and the other at a reference photodiode. We viewed the eye tracker signal (which passed through the ASL-210 electronics, filtering off) and the reference photodiode signal with a two channel oscilloscope, and observed their temporal offset. Delays introduced by the eye-tracker were about 11 ms. A Masscomp MC-5500 lab computer timed events with 1 ms resolution, giving a total eye position signal delay of about 12 ms. Therefore, with the eye moving at maximum velocity, around 500°/s, on-line estimates of eye position lagged true position by about 6°. Except during saccades, the timing delays did not cause significant errors in eye position. Therefore, we can only assert that probe flashes fell on intended retinal loci before and after saccades.

Probe flashes (6000 cd/m^2, 1/4 ms) were produced by 120 red LEDs separated by about 1/2° mounted horizontally in a curved plywood surface. Above and below the LEDs were strips of carbon-impregnated rubber, which with a copper thimble worn on the subject's right index finger, was read by the computer to determine manual pointing directions. A virtual sound source was superimposed on the central LED by placing speakers above and below it. Auditory saccade targets were similarly placed to the left and right. Experiments were conducted in complete darkness. Subjects were light-adapted at the outset, and were allowed to dark-adapt during the 10–15 min of a block of trials.

2.2. Procedure

On each trial subjects fixated a central auditory target. One to two seconds after the subject pressed a ready button, an auditory cue, randomly to the left or right, beeped to elicit the perturbing saccade (the saccade associated with the EEPI shift we seek to measure). In practice trials prior to the experiment, subjects were told when their saccades were smaller than desired or too large for the apparatus. Subjects made approximately 12° saccades in the cued direction. A probe flashed before, during, or after each saccade. In separate blocks, and usually separate days, subjects either pointed with unseen hand to the probe, or looked back to its perceived location. When hand pointing, subjects were required to maintain gaze within 3° of the end point of the initial saccade (Fig. 1). When gaze pointing, subjects pressed a button to indicate they were looking in the perceived direction of the probe, and that eye position was saved by the computer.

The computer aborted trials for a variety of reasons, including blinks during the trial, double saccades, eye drifts from fixation spots, saccades in the wrong direction, and saccades that were too small ($< \sim 4°$) or too large ($> \sim 20°$). Blocks of trials were scheduled for 75 successful trials, and aborted trials were rerun until 75

successful trials or 112 total trials were completed (~ 10–15 min).Probes were positioned relative to the current on-line estimate of gaze direction, either on gaze or ± 10° horizontally from gaze. Saccade direction, probe eccentricity, and the time of probe presentation were chosen randomly on each trial. On 20% of trials (eye-hand coordination trials), the probe flashed 1 s after the saccade cue, or approximately 800 ms after the saccade. On these trials, the LED at the probe location was re-illuminated after the pointing response. Also, with hand pointing, an LED attached to the pointing finger was lit after the finger touched the board, whereas with gaze pointing the LED in the direction pointed to was lit after the trial. Feedback was provided only on these non-perisaccadic trials, when EEPI reached a stable postsaccadic value. Feedback trials helped reduce disorientation from being kept in the dark, and encouraged accurate pointing.

2.3. Subjects

One informed (CB, an author), and two naive (AP and WC) subjects served in these experiments. Naive subjects gave informed consent and were paid for their time. The data re-analyzed from Miller (1996) came from six different subjects.

2.4. Data analysis

Probe presentation and pointing were analyzed relative to the beginning of saccade, removing the dependence of probe and pointing positions on initial eye position.

A three piece-linear function was fit to the data and the parameters of the fit used to define the starting and ending times of relocalization.

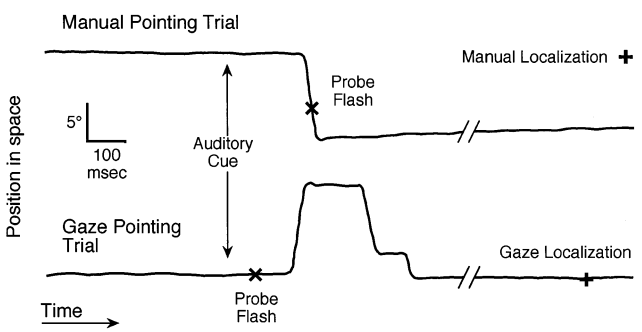

Fig. 1. Manual pointing and gaze pointing trials. Eye position traces are shown for a manual pointing trial (top) and a gaze pointing trial (bottom). In both examples the probe flash is presented on fovea. In the manual pointing example, the subject makes a leftward saccade, and holds the postsaccadic position while pointing with unseen hand ~ 5° right of the probe location. In the gaze pointing example, the subject makes a rightward perturbing saccade, then executes two saccades, accurately localizing the probe, and ends the trial by signaling completion with a button press.

Signal delays in the ASL-210 eye tracker had negligible effect on the data during fixation, but introduced significant errors in probe positioning during a saccade. Locations relative to gaze were corrected off-line by adding to probe and pointing locations the difference between the on-line estimate of eye position and eye position 12 ms later. Figs. 2–4 show examples of corrected and uncorrected data.

3. Results

3.1. Manual versus gaze pointing EEPI

Saccade sizes varied in response to the auditory cue, averaging 10–12°, with standard deviations (SDs) of 2.2–2.6° (Table 1). Perturbing saccades in manual and gaze pointing sessions were similar. Probes were always presented relative to gaze direction, therefore probe positions exhibited the same variability as saccades. Only saccades between 6 and 16° were analyzed.

Figs. 2–4 show representative pointing data for three subjects. Figs. 2 and 3 show manual pointing for subjects WC and AP, respectively, and Fig. 4 shows gaze pointing for subject CB. In all cases, the cloud of data points begins to shift in the saccade direction before the saccade, and does not reach a stable value until after the saccade. The data points in Figs. 2–4 have been corrected for the 12 ms apparatus delays. Moving averages for the corrected and uncorrected data are shown for comparison. Before and after the saccade, correction does not affect the data. During the saccade, however, the bias due to equipment delays is evident, and would lead to the conclusion that remapping of space begins later in time than it actually does.

Fig. 5 is a summary of all rightward saccades for manual and gaze pointing by subject CB. If he were accurate, each set of localizations would fall on the corresponding probe position curve. Substantially before and after the saccade, most subjects showed a characteristic bias in pointing. In Fig. 5, for example, the subject tended to point to the left of targets for manual pointing, particularly when probes were presented postsaccadically. Consistent saccade-related biases are evident in Fig. 5, as the localization curves shift in the saccade direction prior to the saccade and reach a stable value 50–120 ms after the saccade.

Fig. 5 also shows the three-piece linear fits, the parameters of which were used to estimate beginning and ending times of spatial remapping. Saccade directions were combined, probe eccentricities recoded as behind, on, or ahead of gaze, and the fitted values averaged across subjects. Fig. 6 summarizes the fitted values. For both eye and hand pointing, remapping is first seen for eccentric probes presented about 60 ms before the saccade, and for probes on gaze presented

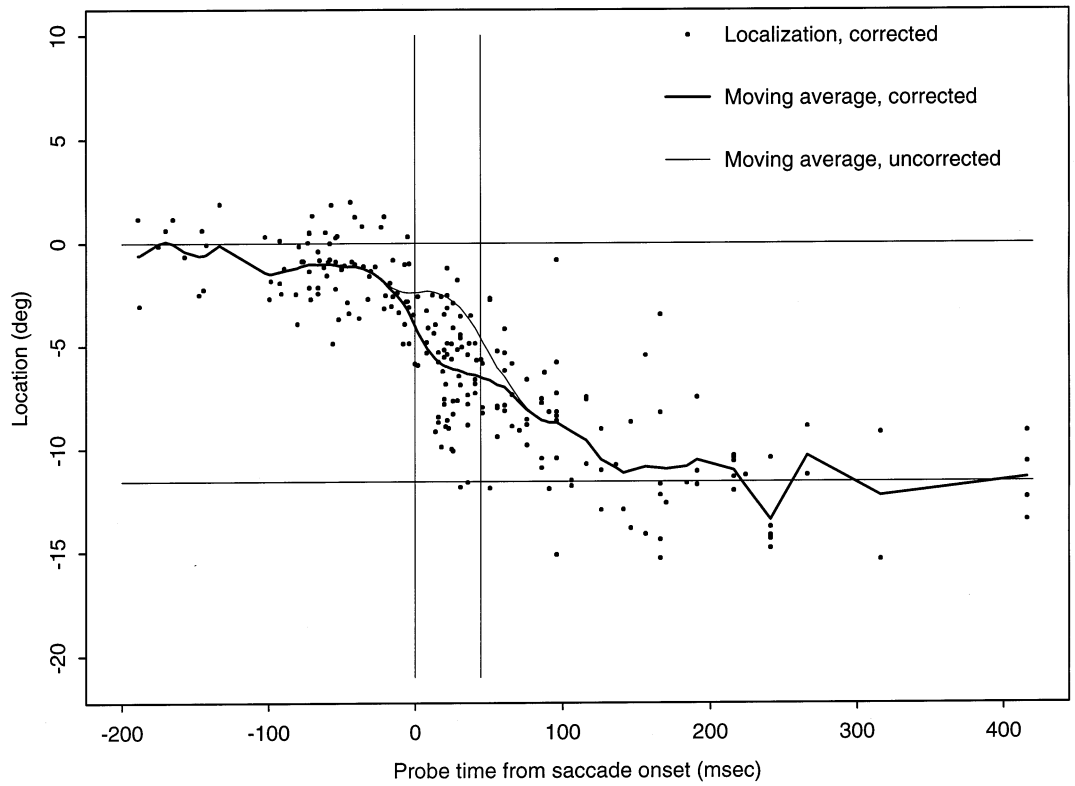

Fig. 2. Manual pointing data from subject WC for probes presented on gaze. All saccades were leftward saccades, and the horizontal and vertical lines show the average beginning and ending eye positions and times for the saccades. Each point is a single pointing response corrected for signal delays, and the thick curve is a moving average through the points. The thin curve is a moving average for uncorrected data (single pointing responses not shown). Additional data from feedback trials, which were clustered around 800 ms after the saccade, are not shown.

about 35 ms before the saccade. An analysis of variance of start of remapping with pointing method (gaze vs. hand) and probe position relative to gaze (behind, on, ahead) found a significant main affect of probe eccentricity ($F = 9.3$, $P < 0.005$, df = 2,30), while the main effect of pointing method and the interaction was not significant.

Remapping of gaze direction continued for 100–170 ms (Fig. 6, right). An ANOVA on the duration of remapping found a significant effect of probe position ($F = 4.14$, $P < 0.05$, $df = 2, 30$). Eccentric probes are remapped with a longer time course then foveal probes. Greater variability in remapping duration compared to the start of remapping is a consequence of analyzing probes relative to presaccadic gaze position, transferring variability to postsaccadic positions. Postsaccadic gaze position also varied due to different saccade sizes.

3.2. Re-analysis of Miller (1996)

Procedures used by Miller (1996), Experiment 2, were identical to the manual pointing procedures here, except probe positions were $-6, 0, 6°$ relative to gaze rather than $-10, 0, 10°$. Results of re-analysis are shown in Fig. 7, and average perturbing saccades are given in Table 1. Overall, remapping started 66 ms before saccades, and required 206 ms for completion.Remapping is seen earlier for probes behind gaze than for probes on gaze ($t = 2.42$, $P < 0.05$, $df = 14$) and required more time than for probes on ($t = 3.7$, $P < 0.01$, $df = 14$) and ahead ($t = 4.1$, $P < 0.01$, $df = 14$) of gaze.

4. Experiment 2: saccades to a central location

Mean EEPI start time found in Experiment 1, 51 ms, is closer to saccade onset than the 100 ms and 180 ms averages reported by Honda (1991), Dassonville et al. (1992) and Honda (1993), respectively. In contrast to those studies, our subjects did not have prior knowledge of saccade direction. It is possible that the earlier EEPI start times reported by Honda (1991), Dassonville et al. (1992) and Honda (1993) were due to oculomotor preplanning, or early shifts of visual attention.

Differences in remapping of different probe positions in space could also be due to a bias to avoid eccentric pointing. After perturbing saccades, the eyes were turned ± 10–$12°$ from straight ahead. Probes in front of gaze were therefore about 20° from straight ahead, and subjects may under-point to these eccentric targets.

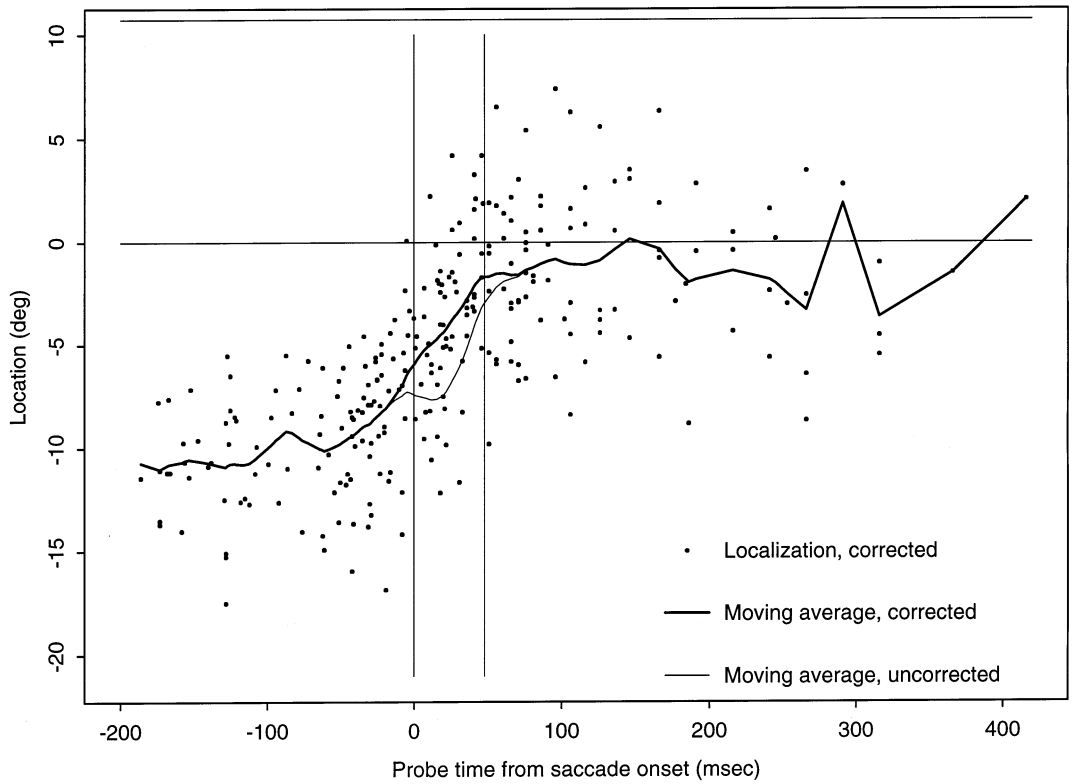

Fig. 3. Manual pointing data from subject AP for probes presented 10° left of gaze. All saccades were rightward saccades. Format as in Fig. 2.

4.1. Procedure

We therefore measured EEPI with initial fixation points $\pm 10°$ from straight ahead and perturbing saccades toward center. Direction of the perturbing saccade was randomized on each trial, but was known to the subject from the location of the initial fixation point. All other methods, procedures, subjects, and apparatus were the same as in Experiment 1.

4.2. Results

Saccade sizes (11–12°) and durations (43 ms) were similar to Experiment 1 (Table 1). Fig. 8 shows the average initiation and duration of remapping, and manual and gaze pointing are again very similar. The average duration of remapping was 148 ms for manual and gaze pointing, which was similar to the 140 ms average in Experiment 1. Probes presented on gaze tend to begin remapping later, closer to saccade onset, than peripheral probes, as in Experiment 1. Average initiation time, 62 ms before the saccade, is similar to the 51 ms initiation time found in Experiment 1.

Localization began shifting for eccentric probes presented about 68 ms before the saccade, and for parafoveal probes presented about 48 ms before the saccade. The corresponding results from Experiment 1 were similar: 60 and 35 ms.

Experiment 2 confirmed the results of Experiment 1 in that differences in remapping for different probe directions follow the same general pattern. Predictability of saccade direction and arm pointing bias had little or no effect on EEPI.

5. Variability analysis

Variability in the timing of shifts in EEPI relative to the saccade, or in visual processing time relative to probe flash presentation, tend to inflate estimates of remapping duration of individual saccades. These sources of variability can be estimated by comparing localization variability during remapping with localization before and after. If EEPI variability is high, we expect a large increase in pointing variability when EEPI changes rapidly.

Parameters of the three-piece linear fit separated each data set into three epochs: before, during, and after saccade-related remapping of retinal locus. We sought to estimate pointing variability during these three periods. To control variability due to different saccade sizes, we analyzed pointing errors. Ideally, we would measure error variability at each point in time. Lacking sufficient data, we fit a curve that accounts for the change in pointing errors due to the saccades, and then analyzed the residual variability. Fig. 9A shows point-

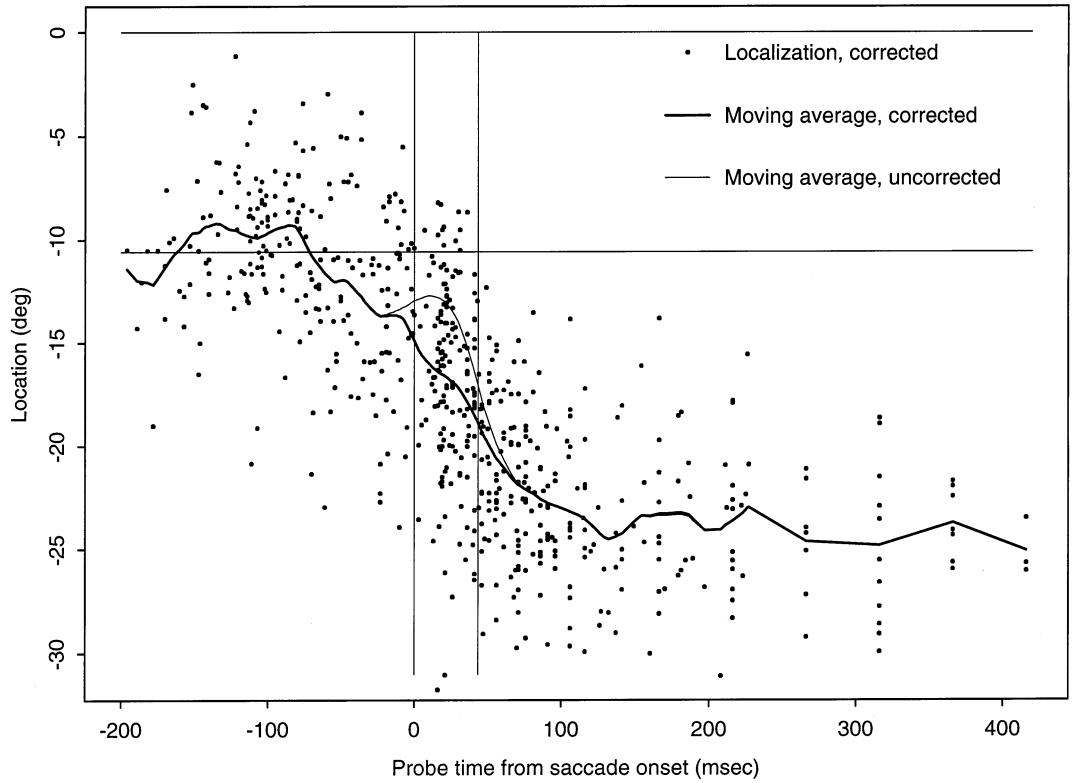

Fig. 4. Gaze pointing data from subject CB for probes presented 10° left of gaze and leftward saccades. Format as in Fig. 2.

ing data in a format similar to Figs. 2–4, with the three-piece linear fit. Fig. 9B shows pointing errors. The curve in Fig. 9B is a weighted moving average, a quadratic fit to successive small temporal windows of data, each shifted 1 data point from the previous window (Cleveland, Grosse & Shyu, 1992). As window size increases, the fitted curve becomes smoother but more biased, particularly near where the errors have extrema. Fig. 9C plots residual errors from Fig. 9B. If the curve fit were unbiased, the residuals would have a mean of zero. Moving averages of the residuals (thin curve, 9C) were generally flat and near zero. Variability of the residuals estimates pointing variability without the constant error introduced by the saccade at each point in time. The thick curve in Fig. 9C is a moving SD, with a window size of 20 ms. SDs increase prior to the saccade, reach a peak shortly after the saccade, and then decline. For each data set, SDs were computed for each epoch (before, during, and after remapping), based on the three-piece linear fits.

Figs. 10 and 11 show SDs (SD) for both experiments, averaged across subjects, for the epochs before, during, and after remapping. ANOVAs for both experiments and both pointing responses showed a significant effect of epoch ($F > 6.0$, $df = 2, 51$, $P < 0.001$, in all cases). Similar trends were found in both experiments and with both pointing responses: SDs were highest during remapping, and SDs before remapping tended to be higher than after. SDs during remapping were always higher than SDs after remapping (t-tests, all Ps < 0.01). SDs before remapping were significantly higher than SDs after (all Ps < 0.05), except with manual pointing in Experiment 1 ($P < 0.2$). SDs during remapping were significantly higher than SDs before remapping for manual pointing in Experiment 1 ($P < 0.01$) and gaze pointing in Experiment 2 ($P < 0.05$).

Our method of measuring variability is vulnerable to several biases. If the fitted local quadratic to the pointing errors (e.g. Fig. 9B) were too smooth (due to a large fitting window), particularly when the average pointing errors are changing rapidly with time, pointing variability would be overestimated. Conversely, if the fitting window were too small, the fit would not show real pointing variability. We selected fitting parameters that produced mean zero residuals during the remapping period (Fig. 9C). Although we found that the absolute values of SD changed with window size, the ratios for the three epochs varied little.

Another bias might arise from using parameters of the three-piece linear fit to delineate analysis epochs. If there is true variability in EEPI, then the fitted parameters give only average starting and ending times for remapping. Hence, the presaccadic and postsaccadic epochs would show increased variability due to EEPI variability, and variability in the middle epoch would be underestimated. However, we found that shifting the

Table 1
Perturbing saccades for all experiments

Saccade size (°)			Saccade duration (ms)		Number of trials
Subject	Mean	Standard deviation	Mean	Standard deviation	
Experiment 1 hand pointing					
CB	12.3	2.4	46	7.9	616
AP	10.9	2.4	48	9.8	353
WC	11.9	2.6	44	7.9	281
Experiment 1 gaze pointing					
CB	11.3	2.6	44	8.2	684
AP	11.3	2.4	51	10.5	354
WC	12.4	2.2	45	7.4	310
Experiment 2 hand pointing					
CB	10.9	2.2	40	6.6	436
AP	11.2	2.4	44	8.8	312
WC	11.5	2.4	42	7.0	284
Experiment 2 gaze pointing					
CB	11.0	2.4	41	7.0	397
AP	11.7	2.4	47	9.8	343
WC	11.3	2.4	42	7.0	319
Miller (1996) manual pointing					
CHD	12.2	2.4	55	11.7	881
JEF	12.1	2.3	41	8.2	354
JMM	10.8	2.5	41	9.8	395
STV	10.6	2.6	48	11.6	782

Saccade sizes and durations were averaged across saccade directions and probe eccentricities. Number of trials is the average number of trials per condition.

epoch boundaries by 10–20 ms had little effect on the ratios of the SDs for the three epochs.

Increased variability during remapping could be due to increased variability in processing the flash, smeared across the retina during saccades. However, our 1/4 ms flashes produced only about 7.5 min arc of smearing, and subjects could not distinguish a probe presented during a saccade from those presented shortly before or after. Further, SDs often began increasing well before the saccade, and reached a maximum after the saccade (Fig. 9C).

5.1. Time course of EEPI for single saccades

We used Monte Carlo simulations to estimate the variability of saccadic EEPI start time (relative to the beginnings of saccade) and the duration of the saccadic shift in EEPI that would produce the mean saccadic EEPI duration (140 ms) and saccadic increase in localization variability (1.35, the ratio of SD during remapping to after remapping), measured in Experiments 1 and 2. Pointing SD was assumed to be 2.0°, the average for pointing after remapping in Experiment 1. We assumed the magnitude of saccadic shifts in EEPI matched the associated shifts in eye position. Using probe timing and saccade distributions similar to those in our experiments, we simulated experiments with different EEPI durations and start time variabilities, and estimated the measured remapping durations and localization SDs that would result. Experiments were simulated with S-Plus software (StatSci, 1995), and the results of individual experiments were analyzed with the same statistical techniques described previously to estimate EEPI time course and variability. Fig. 12 shows the combinations of saccadic EEPI durations and start time SDs that were consistent with our data. In order to obtain a mean EEPI duration of 140 ms, our simulations showed that EEPI start time variability must decrease as EEPI duration increases, as shown (solid line). To maintain the measured ratio of localization variability of 1.35, EEPI variability must increase as EEPI duration increases, as shown (dotted line). The combination of saccadic EEPI duration and start time SD consistent with our mean data occurs where the curves intersect. Thus, we estimate true saccadic EEPI duration to be 135 ms, and EEPI start time SD to be 18 ms.

6. General discussion

We here discuss the present results in the context of other studies that controlled visual referents, and argue

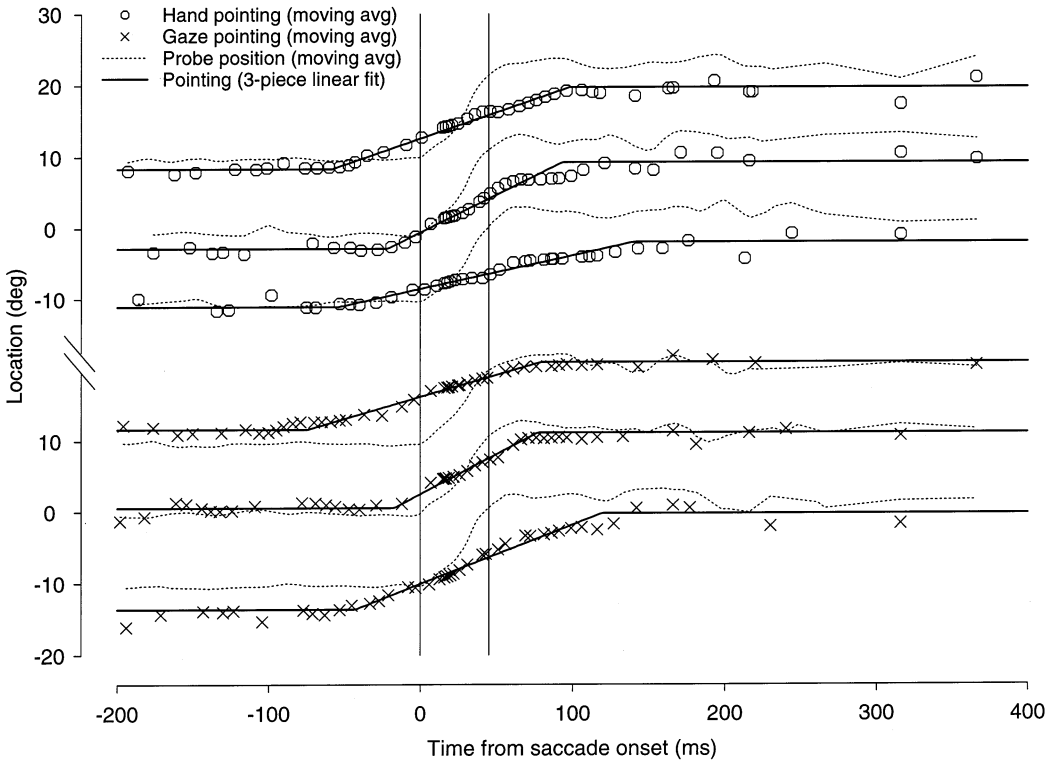

Fig. 5. Localization data for manual pointing (three upper sets of curves and symbols) and gaze pointing (three lower sets) for rightward saccades and probe eccentricities of -10, 0 and $+10°$. Symbols are moving averages of pointing responses, and the associated dotted line is a moving average of probe positions. Solid line is a three-piece linear fit to pointing data. Vertical lines are the beginning and average ending times for the saccades. Subject CB.

that there is now general agreement on EEPI parameters, in that remaining differences across studies can be reasonably attributed to differences in target luminance and light adaptive state of the eye. Finally, we discuss the issue of 'centrality' in visuomotor organization.

6.1. When do saccade related shifts in EEPI begin?

For both manual and gaze pointing, we found that EEPI begins to shift approximately 50 ms before the saccade, compared to 100 ms found by Honda (1991) and Honda (1993) and 180 ms found by Dassonville et al. (1992). These differences could be due to differences in light adaptive states of subjects and probe flash luminance: a delayed retinal signal would interact with

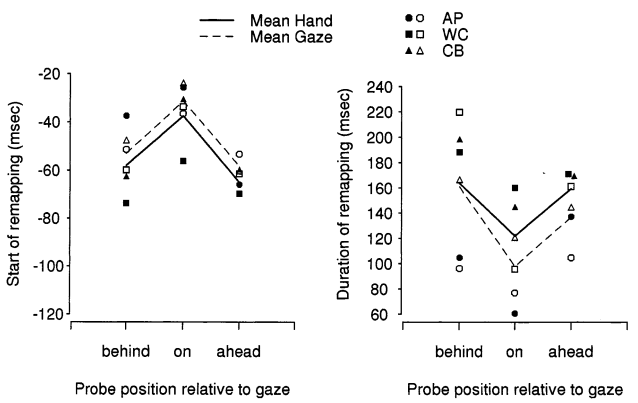

Fig. 6. Left: start of remapping relative to beginning of saccade. Right: duration of remapping. Lines are means. Points are results from individual subjects, averaged over leftward and rightward saccades. Solid lines and closed symbols are hand pointing, broken lines and open symbols are gaze pointing.

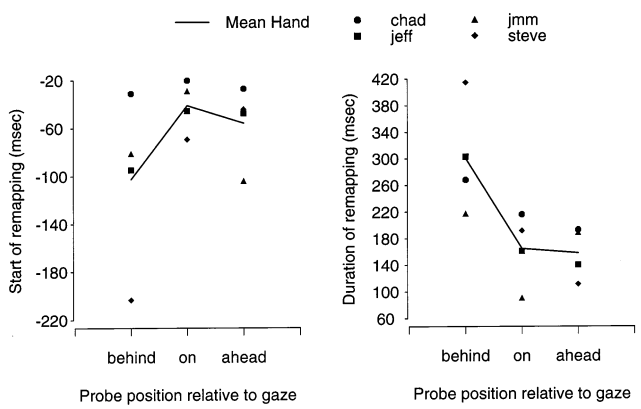

Fig. 7. Re-analysis of data from Miller (1996). Left: start of remapping relative to beginning of saccade. Right: duration of remapping. Lines are means. Points are from individual subjects, averaged over leftward and rightward saccades.

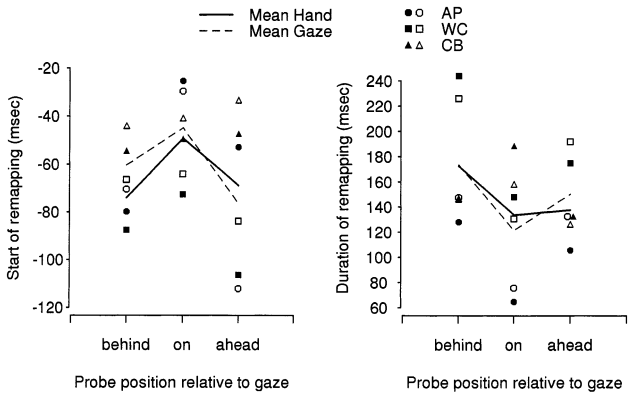

Fig. 8. Left: start of remapping. Right: duration of remapping. Lines are means. Points are results from individual subjects, averaged over leftward and rightward saccades. Solid lines and symbols are hand pointing, broken lines and open symbols are gaze pointing.

a later phase of the EEPI signal, causing localization as a function of target presentation time to shift earlier. Our subjects (and those of Miller (1996)) pointed to bright 6000 cd/m^2, 1/4 ms probe flashes, and worked at intermediate levels of dark-adaptation. Honda used dimmer, 40 cd/m^2, 2 ms flashes with subjects presumably at intermediate levels of dark adaptation, and Dassonville et al. (1992) used very dim, 0.015 cd/m^2, 2 ms flashes with dark-adapted subjects. Increases in dark adaptation and decreases in flash luminance both increase retinal processing time (Lennie, 1981; Lankheet, Rowe, Van Wezel & Van de Grind, 1996), causing retinal signals to interact with later phases of EEPI, so that EEPI appears to shift earlier. Depending on stimulus intensity and dark adaptation, retinal ganglion cells respond 50–300 ms after stimulus presentation (Lennie, 1981), which includes the range of times by which EEPI change precedes saccades in the studies under consideration. Dimmer probes and dark adaptation may also increase sensory timing variability, which would shift measured EEPI start times earlier. Thus, we would expect Dassonville et al.'s subjects to show the earliest EEPI shifts, our subjects to show the latest, and Honda's subjects to fall in between, which is what is found.

We know of two experimental attempts to demonstrate effects of background or probe flash luminance on saccadic localization. Nagle and Bridgeman (1983) varied ambient illumination over two log units, and could find no effect on intrasaccadic displacement thresholds. However, since saccadic suppression of displacement occurs for flashes up to 50 ms before, and 50 ms after a saccade (Bridgeman, Hendry & Stark, 1975), only large changes in latency would push the registered time of the stimulus outside the suppressive range. Skavenski, Cumming and Hansen (1983) found no effect of target luminance in an intrasaccadic manual pointing task, but this study (reported in abstract) appears to have used procedures that previously failed to show errors in intrasaccadic pointing (Hansen & Skavenski, 1977).

A reasonable conclusion, therefore, is that the localization mechanism combines EEPI with sensory information delayed by retinal processing. The similarity of results in Experiments 1 and 2 show that predictability of saccade direction has little or no effect on associated EEPI. Other experimental differences, such as visible fixation and saccade targets, as well as individual subject differences (Miller, 1996), may, of course, be relevant.

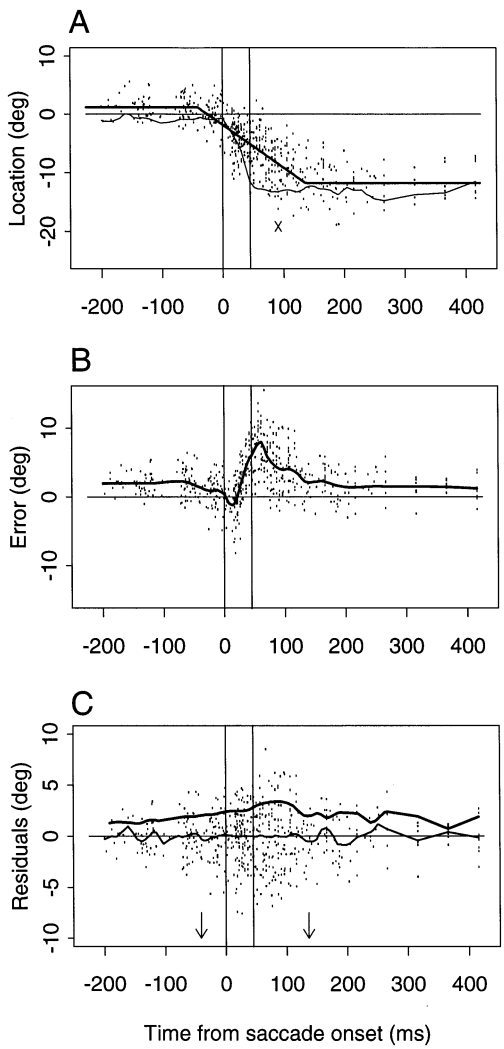

Fig. 9. Example of the analysis of pointing variability. (A) Localization for leftward saccades, probes on gaze, for subject CB, with three-piece linear fit to localization data (thick line) and a moving average of the probe positions (thin line). Outliers (more than three SDs from an initial fitted line) are marked by Xs and were removed prior to analysis. Vertical lines mark the beginning and average ending times of the saccades. (B) Pointing errors for the same data set. The curve is a local quadratic fit (see text). (C) Residuals from the fit in middle panel. The thin curve is a moving average of the residuals, and the thick curve is a moving SD of the residuals, each using a 20 ms window. Arrows on the abscissa mark beginning and ending times of remapping based on the three-piece linear fit shown in top panel.

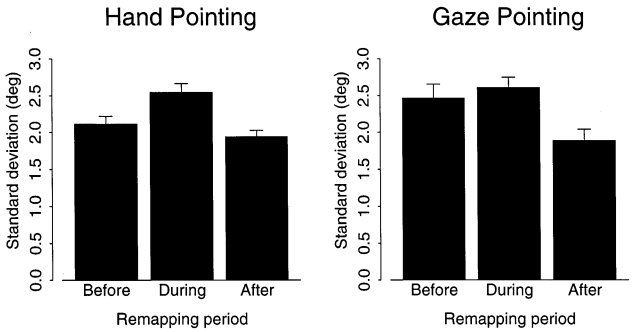

Fig. 10. SDs of pointing for Experiment 1. Left: hand pointing. Right: gaze pointing. Time was divided into three epochs based on the three piece linear fits. Each bar is the average SD for that epoch over three subjects. Error bars are 1 S.E. of this mean.

We also found that EEPI start time and visual processing combined have a SD of 15–20 ms. Although EEPI and visual processing variability cannot be distinguished in our data, there is reason to think that a significant part of this variability is due to visual processing. For example, Lennie (1981) found that the SD of mean time for ganglion cells to respond to 50 ms duration flashes ranged from 10 to 25 ms.

6.2. Duration of saccadic EEPI

Our best estimate of the duration of saccadic EEPI in the present study (adjusted for the 5–10 ms overestimate due to variability) is 130–135 ms, or about 3 times the mean duration of our saccades (45 ms). Similarly analyzed, the data of Miller (1996) show that EEPI shifts over a period 4.4 times saccade duration (45 ms in that study). Honda (1991) shows EEPI duration 5.3 times saccade duration (38 ms), and Dassonville et al. (1992) show EEPI durations 3.8 times saccade duration (64 ms).

Previous studies of EEPI could not distinguish damped EEPI from fast and variable EEPI. EEPI could, for example, shift instantaneously from pre- to post-saccadic values, with variability in oculomotor and visual processing causing EEPI to appear damped in averages over many localization trials. Our finding of

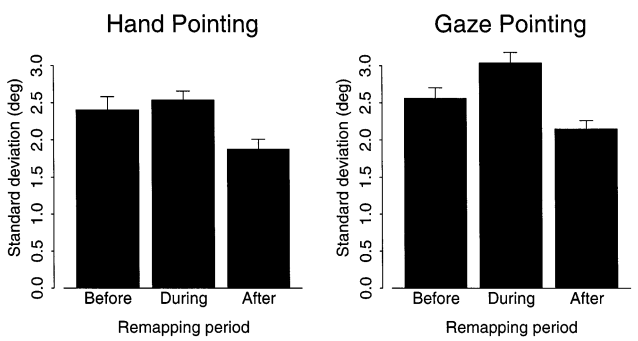

Fig. 11. SDs of pointing for Experiment 2. Format as in Fig. 10.

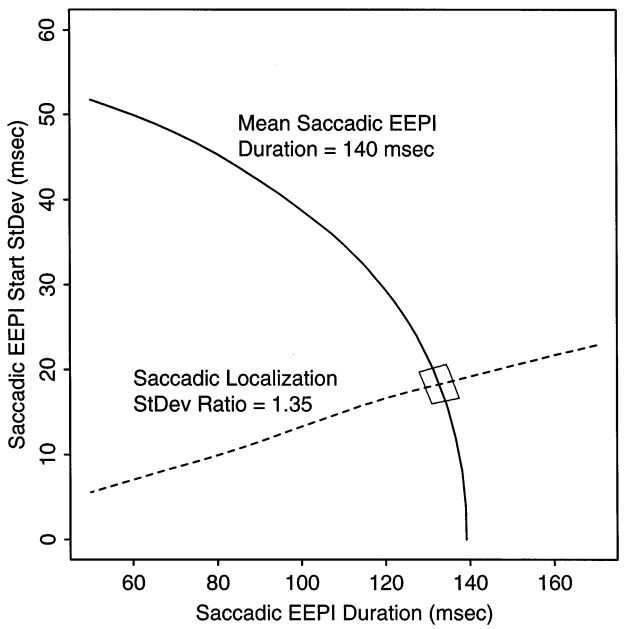

Fig. 12. Results of simulations showing the combinations of saccadic EEPI duration and start time SD needed to produced mean saccadic EEPI (solid line) and mean ratio of intrasaccadic to postsaccadic SD (dotted line) obtained in our experiments. The box encloses the 99% confidence region for saccadic EEPI duration and SD of saccadic EEPI start.

low localization variability during remapping, and thus low EEPI start time variability, confirms that damped EEPI accompanies each individual saccade.

Why does EEPI change so slowly compared to its saccade? Supposing a simple efference copy model, damping would be determined by the process in which EEPI, along with retinal image information, was used to determine a pointing response. Coordination of saccadic eye movement with its EEPI would also depend on delays and filtering in the pathway from oculomotor command, through the brainstem, to the viscous plant. Grüsser et al. (1987) quantified the common observation that afterimages appear to lag behind perceived eye movements. Movement of an afterimage and perceived eye movement both involve EEPI, but only the former involves applying EEPI to retinal image information. This suggests that the process of combining EEPI with retinal information introduces damping.

6.3. Remapping depends on retinal locus

Saccadic remapping of probes presented on or near the fovea appears to begin about 20 ms later than remapping of eccentric probes. Focal attention biases temporal order judgments such that stimuli at attended locations may be perceived 30–70 ms earlier then stimuli at non-attended locations (Hikosaka, Miyauchi & Shimojo, 1993). Our subjects began each trial by fixing straight ahead in complete darkness. This difficult task,

we expect, required that attention be strongly focused. For early presaccadic stimuli, at least, probes on gaze were presented in a region where attention was focused. If attention sped probe flash processing, it would interact with an earlier phase of EEPI, and would appear to begin remapping later, closer to saccade onset, as our results show.

Ross et al. (1997) and Morrone et al. (1997) reported compression of visual space previous to saccades and around their visible targets. Our data show that remapping of probes ahead of gaze begins earlier than of probes on gaze, that is, an expansion of space in front of gaze. However, Ross et al. used continuously visible fixation and saccade targets, and visible backgrounds, whereas we used no visible targets or referents. Shifts of attention to saccade targets precede eye movements (Kowler, Anderson, Dosher & Blaser, 1995; Deubel & Schneider, 1996), and attention is focused on initial fixation locations prior to saccades. Perhaps in Ross et al. the visible saccade target was the focus of attention, which may have biased location judgments. A biasing affect of the saccade target may also be seen by the relatively small variability in localization observed by Ross et al., compared to our data and that of others (Dassonville et al., 1992). Thus, subjects may have localized the probe targets relative to the visible saccade goal, rather than egocentrically. Presence of a visible background also may have contributed to their results. Morrone et al. (1997) simulated the visual affects of saccades by moving the display at saccadic velocities, and showed that mislocalizations can be greater prior to simulated saccades than prior to real saccades. We propose that with real saccades, but not simulated saccades, saccadic EEPI is able to partly compensate for retinal image movement. While we cannot account for all of the differences in our data from Ross et al. (1997) we suspect that the Ross et al. results show contributions of both retinal and extraretinal mechanisms of egocentric localization, whereas our results isolate extraretinal mechanisms.

6.4. Manual and gaze pointing use similar EEPI

The main result of this study is that manual pointing and gaze pointing use similar damped EEPI. Thus, inconsistencies in the saccadic pointing literature are not intrinsic to the pointing response used. This result is consistent with the hypothesis that both manual and gaze pointing rely on a common representation of space. Since eye and hand movements are often directed to the same location, linking the two might simplify or enhance localization. Indeed, dissociating the responses can require long practice, as in learning to touch-type. De Graaf, Pelisson, Prablanc and Goffart (1995) reported that saccadic gain adaptation transfers to manual pointing, and Van Donkelaar, Fisher and Lee (1994) found that adaptive increases in pursuit gain increase the gain of manual tracking. Nemire and Bridgeman (1987) reported that multiple full-field saccades during the interval between presentation of a probe target and a cue to point 20 s later similarly degraded reaching and gaze pointing. Such results suggest a common, plastic representation of space.

Nevertheless, it remains possible that, instead of a common spatial representation, manual and gaze pointing systems use different but similarly calibrated representations of space, with different EEPI signals provided to each motor system. Many cortical retinotopic maps have been described (for review, see Moschovakis & Highstein, 1994), but only a few head-centric maps (e.g. Schlag & Schlag-Rey, 1987). Regions in pre-motor cortex have visual receptive fields defined relative to hand positions (Gentilucci, Fogassi, Luppino, Matelli, Camarda & Rizzolatti, 1988; Graziano, Yap & Gross, 1994; Fogassi, Gallese, Fadiga, Luppino, Matelli & Rizzolatti, 1996). Cells in oculomotor centers, such as the frontal eye fields (Bruce & Goldberg, 1984) and superior colliculus (Robinson, 1972), have receptive fields defined relative to eye position. Compared to transforming a complex central representation of space, it may be sufficient, and faster, to transform only the retinal loci containing the target, or at the motor end, only the coordinates of the pointing hand or eye.

6.5. Perceptual EEPI versus motor EEPI?

Before there was evidence of large errors in manual and gaze pointing EEPI, it seemed that motor systems used accurate EEPI, whereas cognitive-perceptual systems (e.g. visual matching and verbal report methods used by Matin and colleagues (Matin & Pearce, 1965; Matin et al., 1969; Matin et al., 1970; Matin, 1976)) discounted EEPI, or used an inaccurate version. This dichotomy gained support from neurophysiologic concepts of multiple visual pathways, such as the 'what' and 'where' pathways proposed by Ungerleider and Mishkin (1982) and the 'what' and 'how' pathways proposed by Goodale and Milner (1992). Other psychophysical results are consistent with the perceptual–motor distinction (Bridgeman, Lewis, Heit & Nagle, 1979; Bridgeman, Kirch & Sperling, 1981), and the notion of different localization mechanisms remains popular (Bridgeman, Van der Heijden & Velichkovsky, 1994).

An early study comparing visual matching and gaze pointing (Miller, 1980) had subjects make saccades and then relocalize the initial fixation point, and concluded that postsaccadic perceptual and motor EEPI were the same. Our present finding that both hand and eye pointing systems express similar EEPI, which is also similar to EEPI measured 'perceptually', favors a 'central sensorimotor system,' but is also compatible with

'coordinated independent systems.' Studies of adaptation and transfer similarly favor a central system (Van Donkelaar et al., 1994; de Graaf et al., 1995). Studies of differential adaptation could provide a strong test of this important organizational distinction.

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